

WATER POTENTIALS OF *SALVIA APIANA*, *S. MELLIFERA* (LAMIACEAE),
AND THEIR HYBRIDS IN THE COASTAL SAGE SCRUB OF
SOUTHERN CALIFORNIA

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ABSTRACT

Shrubs in the genus *Salvia* are often dominants in Coastal Sage Scrub communities throughout southern and central California. *Salvia mellifera* E. Greene (black sage) tends to be more abundant near the coast with a more northerly distribution, whereas *S. apiana* Jepson (white sage) tends to occur farther inland and ranges much farther south. In areas of local sympatry in southern California, *S. apiana* is more frequently observed on south-facing slopes. It has been suggested to be better able to withstand drought conditions than *S. mellifera*, because *S. apiana* occurs in what appear to be more xeric sites. In addition, in areas of sympatry, somewhat fertile, morphologically intermediate hybrids form. We tested the hypothesis that *S. apiana* is better able to withstand drought than *S. mellifera*, and that hybrids are physiologically intermediate, by measuring predawn and midday water potential every month over 15 months at a site in the Santa Ana Mountains. *Salvia apiana* had statistically higher water potentials than *S. mellifera* during summer drought, and the hybrid exhibited intermediate values. The ability of *S. apiana* to maintain water potentials of 3 to 4 MPa greater than *S. mellifera* supports the hypothesis that *S. apiana* can better avoid summer drought. This difference in water relations may account in part for the distributional patterns of these two species.

Salvia apiana Jepson (White Sage) and *S. mellifera* E. Greene (Black Sage) are widespread species of summer deciduous shrubs that often dominate Coastal Sage Scrub (CSS) communities of central and southern California (Epling 1938; Harrison et al. 1971; Axelrod 1978; Kirkpatrick and Hutchinson 1980; Westman 1981) [botanical nomenclature follows Hickman (1993)]. The center of the geographical range of *S. apiana*, however, is over 300 km south of that of *S. mellifera*; where their ranges overlap in southern California, *S. apiana* can occur about 15–30 km farther inland extending into the western margins of the Mojave and Colorado deserts (Fig. 1). Over much of its range, therefore, *S. apiana* experiences a hotter, drier climate than *S. mellifera*. In areas where they are locally sympatric, *S. apiana* exhibits greater relative abundance on more xeric sites (interior, south-facing, well-drained, etc.); whereas, *S. mellifera* is often relatively more abundant in somewhat less xeric sites (Epling 1947; Anderson and Anderson 1954; Kirkpatrick and Hutchinson 1980; Westman 1981; DeSimone and Burk 1992). These distributional differences suggest that *S. apiana* can somehow better withstand summer drought conditions than *S. mellifera*, but this idea has not been tested.

Somewhat fertile hybrids will form where *S. apiana* and *S. mellifera* are sympatric (Epling 1938; Grant and Grant 1964) and the hybrids exhibit clearly intermediate reproductive and vegetative characteristics (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987). The large leaves of *S. apiana* are covered with dense, white pubescence, the smaller, narrower leaves of *S. mel-*

lifera are glabrous and green, and those of the hybrid are intermediate in size, shape and degree of pubescence (Webb and Carlquist 1964). Survival of these hybrid populations primarily at disturbed sites has been used to infer that the hybrids are less competitive than either parent in the absence of disturbance (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987), however, very little is known of the physiological ecology of hybrid plants growing in natural environments (Rieseberg 1995).

Much of the original CSS habitat has been adversely impacted by agriculture and urbanization and is being reduced to increasingly smaller habitat islands (Westman 1981; O'Leary 1990). In spite of these environmental concerns, very little data exists on the physiological ecology of the summer deciduous plants composing this rapidly disappearing community (Mooney 1977; Westman 1981). The purpose of this study is to investigate seasonal patterns of water potential of *Salvia apiana*, *S. mellifera* and their hybrids in a CSS site where they co-occur. Studying these taxa in a single site where they all experience essentially the same rainfall and environmental conditions is a useful investigative approach, since differences in water potentials will indicate ecophysiological differences in drought response. The specific null hypothesis we tested was that water potentials of these three taxa would not differ (H_0 : *S. apiana* = hybrid = *S. mellifera*). If *S. apiana* can maintain significantly more positive water potentials while receiving the same amount of precipitation, this would support the hypothesis

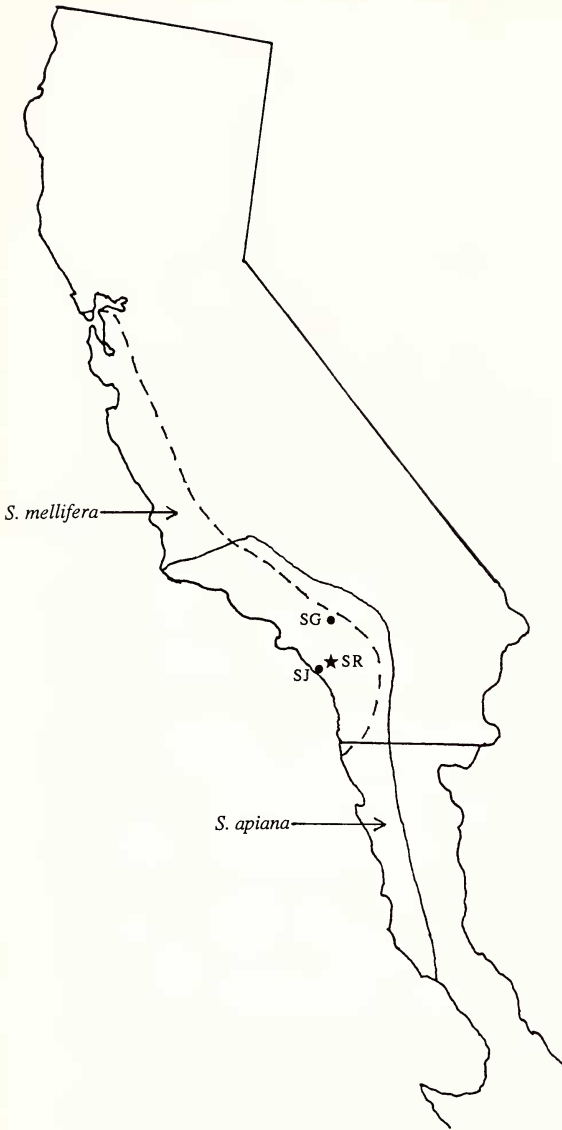


FIG. 1. The geographical ranges of *Salvia apiana* (solid line) and *S. mellifera* (dashed line) based on Figure 1 in Epling (1947), and data in Epling (1938) and Jepson (1939). The primary study site was located at Starr Ranch National Audubon Sanctuary (SR), while secondary sites were located in the San Joaquin Hills (SJ) and in San Gabriel Canyon (SG).

that *S. apiana* is better able to avoid summer drought than *S. mellifera*.

METHODS

The study site was located at Starr Ranch National Audubon Sanctuary in southeastern Orange Co., CA (Fig. 1) which has large stands of relatively intact CSS (DeSimone and Burk 1992). The mediterranean climate is characterized by warm (21°C mean air temperature), dry summers and cool

(12°), wet winters with an annual precipitation of 36 cm with most falling from November to April. The primary research site (ca. 1.5 ha) was located at 370 m elevation on a west-facing slope (290° azimuth, 19° slope). The well-drained soils throughout the site are from the Gabino gravelly clay loam series (DeSimone and Burk 1992). The vegetation at the time of the study was about 15 years old and was dominated by *Artemisia californica* Less. and codominated by both species of *Salvia*, several other species of shrubs, and by a fairly high cover of native, perennial bunchgrass (*Nassella* sp.). The *Salvia* taxa were distributed throughout the site with no apparent differences in microhabitat selection.

In early February 1995, 10 sets (=blocks) of plants were selected, with each block containing one individual each of *Salvia apiana*, *S. mellifera*, and their hybrid all growing within 10 m of one another. Individuals within each block of plants were thus experiencing environmental conditions as similar as is possible in the field. Plants were assigned to respective taxa based on inflorescence structure, and on the size, shape and extent of pubescence of leaves (see Epling 1947; Anderson and Anderson 1954; Webb and Carlquist 1964; Meyn and Emboden 1987). Based on these criteria the hybrids appeared to be F_1 's or first generation backcrosses toward *S. mellifera*. A random sample of 5 of these sets was selected for water potential measurements. Predawn and midday water potentials (WP) were measured monthly on 3 shoots per plant using a Scholander-style pressure chamber (Ritchie and Hinckley 1975). Every 2–3 months we switched to the other 5 sets of plants to minimize possible effects of harvesting shoots on plant vigor. Rainfall data were obtained from a gauge at the Starr Ranch headquarters about 1 km away and 70 m lower in elevation.

To confirm the generality of WP responses obtained in the primary site at Starr Ranch, WP was also measured in the summer of 1996 (23–25 June, 10 weeks since last spring rain) at two additional sites in southern California. The San Joaquin Hills site was located about 20 km SW near the Pacific Ocean and the San Gabriel Canyon site was about 60 km NNE in the interior foothills of the San Gabriel Mountains. Mean midday WP of *Salvia apiana*, *S. mellifera*, and their hybrids was measured on 3 shoots from five plants of each taxa except at the San Gabriel Canyon site where only three hybrid individuals could be located.

To test for differences among species (=taxon effects) and blocks (=microsite effects), data were analyzed using two-way analysis of variance (GLM procedure) on raw data since the data met the assumptions for homogeneity of variance (Levene's test, Minitab 1995). Microsite effects were not significant so all subsequent analysis was based on one-way analysis of variance (one-way procedure) and when significant ($P < 0.05$) taxon-level differ-

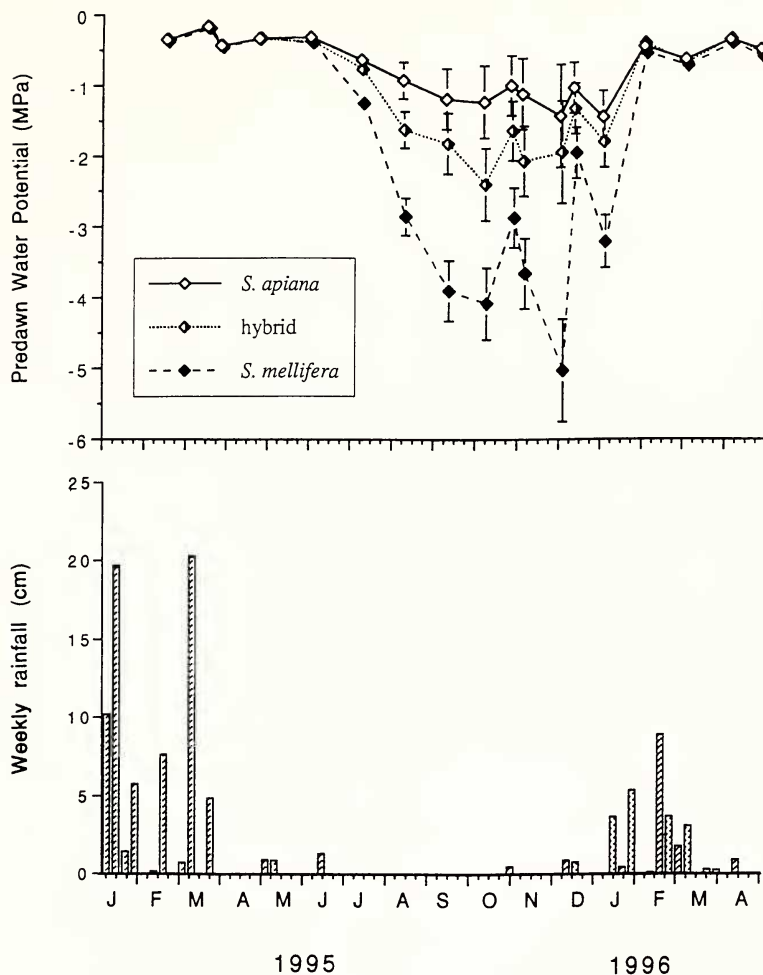


FIG. 2. Rainfall and predawn water potential of *Salvia apiana*, *S. mellifera*, and their hybrid at the Starr Ranch site. Rainfall is expressed as weekly total (cm), and water potential as the mean (± 1 pooled SD) of five plants of each taxa, from January 1995 through April 1996. When no error bars are observed the pooled SD is smaller than the plotted symbol.

ences were detected, Fisher's aposteriori test was used to compare means (Minitab 1995). Data are expressed as means (± 1 pooled standard deviation; $1 \text{ SD}_{\text{pooled}} = \sqrt{\text{mean square error from the ANOVA}}$).

RESULTS

From February through early June of 1995 there were no significant differences in predawn water potential (WP) among taxa, with WP of all taxa being greater than -0.5 MPa (Fig. 2). After the last rain of the season, WP of all taxa started to decline as water loss began to exceed uptake. During summer drought conditions, *S. mellifera* experienced more negative WP than *S. apiana* and the hybrids were intermediate. On all 9 sampling dates from mid-July through early January 1996, WP differed significantly ($P < 0.01$) among taxa and the mean values always ranked in the order of *S. apiana* >

hybrid > *S. mellifera*. Following an early autumnal rain of 0.46 cm on 2 November, WP of all taxa rapidly increased within 36 hours (Fig. 2). With no additional rain for two months, WP again declined showing the same pattern of differences among taxa. By early December, WP of *S. mellifera* was 3.6 MPa less than *S. apiana*. This same pattern of increasing and decreasing WP occurred again after a mid-December rain and a subsequent month-long dry period. After the middle of January 1996, relatively large rainstorms occurred almost every week and by early February WP of all taxa increased to above -0.5 MPa as had occurred the previous spring. There were no significant differences among taxa during the wet period from February through the end of the study in April 1996 (Fig. 2).

The seasonal pattern in midday water potentials among these three taxa throughout the study was

TABLE 1. MEAN MID-DAY WATER POTENTIALS (MPa) OF *SALVIA APIANA*, *S. MELLIFERA*, AND THEIR HYBRID IN LATE JUNE 1996 AT THREE DIFFERENT SITES: STARR RANCH, SAN JOAQUIN HILLS, AND SAN GABRIEL CANYON (SEE METHODS). Overall significance levels (P) for taxon effects were determined by ANOVA; means within a site sharing the same superscript did not differ significantly ($P < 0.05$) as determined by Fisher's a posteriori comparison of means.

	Starr Ranch	San Joaquin Hills	San Gabriel Canyon
<i>S. apiana</i>	-1.86 ^a	-1.87 ^a	-1.15 ^a
Hybrid	-2.90 ^b	-3.07 ^b	-2.64 ^b
<i>S. mellifera</i>	-3.46 ^b	-4.76 ^c	-3.10 ^b
Pooled SD	±0.49	±0.82	±0.42
P	<0.001	<0.001	<0.001

the same as for predawn values, with all taxa experiencing midday depressions in WP of about -0.4 to -0.6 MP relative to predawn (data not presented). In addition, to confirm the generality of the results obtained at the Starr Ranch site, WP was measured during the early summer drought (23–25 June 1996, 10 weeks since last spring rain) at two additional sites in southern California. At all three sites there were significant differences among taxa, with higher WP exhibited by *S. apiana*, intermediate values by the hybrids, and the most negative values by *S. mellifera* (Table 1).

DISCUSSION

When these taxa co-occur at the same site, *S. apiana* maintains a significantly higher WP during summer drought than *S. mellifera* (Fig. 2, Table 1). The values of WP of *S. mellifera* obtained here are similar to other published reports of decreases from -5 to -9 MPa by the end of the summer drought (Mooney 1977; Gill and Mahall 1986; Kolb and Davis 1994). In San Diego Co., WP for *S. apiana* had decreased to -3.7 MPa at the end of summer drought, whereas WP in *Artemisia californica*, another dominant at many CSS sites, decreased to < -6.5 MPa (Poole and Miller 1975). This limited data from the literature on WP of CSS species also suggest that *S. apiana* does not experience WP as negative as *S. mellifera* or *A. californica*. *Salvia apiana* appears to be able to "avoid" summer drought relative to *S. mellifera*, which appears to be able to "tolerate" prolonged periods of very low WP (avoidance/tolerance *sensu* Mooney and Dunn 1970). The ability of *S. apiana* to maintain much higher WP during summer drought could account in part for distribution patterns of these species, apparently permitting survival of *S. apiana* in drier sites.

The functional basis for these different responses to summer drought does not appear to be related to summer deciduousness. By the end of summer, *S. apiana* retains ca. 50% of its spring-time leaf area, whereas *S. mellifera* becomes close to fully deciduous (Gill and Mahall 1986). Another possible explanation could be rooting depth. While most CSS species are apparently shallowly rooted, very little quantitative data is available. Hellmers et al. (1955) present limited data which indicate that *S. apiana*

($n = 1$) may have slightly greater rooting depth than *S. mellifera* ($n = 2$), 1.5 m compared to 0.6 m deep, respectively. The greater rise in WP immediately after the first rain of the season by *S. mellifera* (Fig. 2) also suggests that at least some of the roots of *S. mellifera* are shallower than those of *S. apiana*; however, it seems unlikely that small differences in rooting depth alone could account for the large differences in WP between the species during summer drought. Perhaps *S. apiana* has more conservative rates of transpirational water loss. Whole-leaf absorptance of photosynthetically active radiation (400–700 nm) is about 0.60 for the whiter leaves of *S. apiana* and almost 0.85 for the green leaves of *S. mellifera* (Ehleringer and Comstock 1989). Lower leaf absorptance in *S. apiana* (pubescent leaves, interior distribution) than *S. mellifera* (glabrous, more maritime) may help reduce leaf temperatures and transpirational demand in ways analogous to pubescent versus glabrous species of *Encelia* (Ehleringer and Cook 1990).

During summer drought, the hybrids exhibited WP intermediate between the parental species (Fig. 2, Table 1). We are aware of few studies on comparative WP of natural hybrids and parental species. In a study of *Arctostaphylos patula* E. Greene (generally more mesic), *A. viscida* C. Parry (generally more xeric), and their hybrids in the Sierra Nevada, the hybrids tended to have WP intermediate between parental species (Ball et al. 1983). The tissue osmotic potentials and elastic modulus of hybrids of two species of *Dubautia* in Hawaii also exhibited values intermediate between parental species, but WP was not measured (Robichaux 1984).

The hypothesis that these hybrids are competitively inferior to the parental species except in disturbed sites (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987) is difficult to test since necessary levels of disturbance were not specified. However, based on seasonal changes of WP at our study sites (Fig. 2, Table 1) it appears that hybrid individuals are not inferior to parental species in terms of competition for soil moisture at least among adult plants. Current hybridization between *S. apiana* and *S. mellifera* has produced individuals that are intermediate relative to parental species in terms of ability to avoid experiencing

very low WP during summer drought. Controlled crosses could help elucidate the genetic basis for the different responses to summer drought of these two important CSS species.

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LITERATURE CITED

- AXELROD, D. I. 1978. The origin of coastal sage vegetation, Alta and Baja California. *American Journal of Botany* 65:117-131.
- ANDERSON, E. AND B. R. ANDERSON. 1954. Introgression of *Salvia apiana* and *Salvia mellifera*. *Annals Missouri Botanical Garden* 41:329-338.
- BALL, C. T., J. KEELEY, H. MOONEY, J. SEEMAN, AND W. WINNER. 1983. Relationship between form, function, and distribution of two *Arctostaphylos* species (Ericaceae) and their putative hybrids. *Acta Oecologica* 4:153-164.
- DESIMONE, S. A. AND J. H. BURK. 1992. Local variation and distributional factors in Californian coastal sage scrub. *Madroño* 39:170-188.
- EHLERINGER, J. H. AND J. P. COMSTOCK. 1989. Pp. 21-24 Stress tolerance and adaptive variation in leaf absorbance and leaf angle. in S. Keeley (ed.), *The California Chaparral: Paradigms revisited*. Natural History Museum of Los Angeles County, Los Angeles, CA.
- EHLERINGER, J. H. AND C. S. COOK. 1990. Characteristics of *Encelia* species differing in leaf reflectance and transpiration rates under common garden conditions. *Oecologia* 82:484-489.
- EPLING, C. 1938. The California Salvias. A review of *Salvia*, section *Audibertia*. *Annals Missouri Botanical Garden* 25:95-188.
- EPLING, C. 1947. Natural hybridization of *Salvia apiana* and *S. mellifera*. *Evolution* 1:69-78.
- GILL, D. S. AND B. E. MAHALL. 1986. Quantitative phenology and water relations of an evergreen and a deciduous chaparral shrub. *Ecological Monographs* 56:127-143.
- GRANT, K. A. AND V. GRANT. 1964. Mechanical isolation of *Salvia apiana* and *Salvia mellifera* (Labiata). *Evolution* 18:196-212.
- HARRISON, A. T., E. SMALL, AND H. A. MOONEY. 1971. Drought relationships and distribution of two mediterranean-climate California plant communities. *Ecology* 52:869-875.
- HICKMAN, J. C., (ed.). 1993. *The Jepson manual*. University of California, Berkeley, CA.
- HELLMERS, H., J. S. HORTON, G. JUHREN, AND J. O'KEEFE. 1955. Root systems of some chaparral plants in southern California. *Ecology* 36:667-678.
- KIRKPATRICK, J. B. AND C. F. HUTCHINSON. 1980. The environmental relationships of California coastal sage scrub and some of its component communities and species. *Journal of Biogeography* 7:23-28.
- KOLB, K. J. AND S. D. DAVIS. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* 75:648-659.
- MEYN, O. AND W. A. EMBODEN. 1987. Parameters and consequences of introgression in *Salvia apiana* X *S. mellifera* (Lamiaceae). *Systematic Botany* 12:390-399.
- MINITAB INC. 1995. *Minitab reference manual*, release 10Xtra. State College, PA.
- MOONEY, H. A. 1977. Southern coastal scrub. Pp. 471-478 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley-Interscience, New York.
- MOONEY, H. A. AND E. L. DUNN. 1970. Convergent evolution of mediterranean climate evergreen sclerophyllous shrubs. *Evolution* 24:292-303.
- O'LEARY, J. F. 1990. Californian coastal sage scrub: general characteristics and considerations for biological conservation. Pp. 24-41 in A. A. Schoenherr (ed.), *Endangered plant communities of southern California*. Southern California Botanists Special Publication #3, Rancho Santa Ana Botanic Garden, Claremont, CA.
- POOLE, D. K. AND P. C. MILLER. 1975. Water relations of selected species of chaparral and coastal sage communities. *Ecology* 56:1118-1128.
- RIESEBERG, L. H. 1995. The role of hybridization in evolution: Old wine in new skins. *American Journal of Botany* 82:944-953.
- RITCHIE, G. A. AND T. M. HINCKLEY. 1975. The pressure chamber as an instrument for ecological research. *Advances in Ecological Research* 9:165-254.
- ROBICHAUX, R. H. 1984. Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrids. *Oecologia* 65:75-81.
- WESTMAN, W. E. 1981. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62:170-184.
- WEBB, A. AND S. CARLQUIST. 1964. Leaf anatomy as an indicator of *Salvia apiana*-*mellifera* introgression. *Aliso* 5:437-449.